

HABITAT CHARACTERISTICS OF *EUTREMA PENLANDII* (BRASSICACEAE) IN THE COLORADO ROCKIES: A STUDY OF ALPINE ENDEMISM

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ABSTRACT

The Mosquito Range of central Colorado contains a number of endemic and disjunct plant taxa. Among these is *Eutrema penlandii* (Brassicaceae), a species with arctic affinities known only from a few populations in the Mosquito Range. Previous studies predicted *Eutrema* was restricted to carbonate bedrock, but we found that an alkaline (carbonate) substrate is not a causative factor in the narrow endemism of this species. Critical environmental parameters include a continual supply of moisture from late snowbeds, and a cold microsite insulated by a bryophyte mat that retains moisture. These factors suggest that the species may be a Pleistocene relict with a currently limited amount of critical habitat. There is cause for concern about the future of this species in light of our climatic uncertainty.

Unusual bedrock often provides habitat for rare alpine plants. Ultramafic, carbonate, and highly mineralized soils in particular are known to be associated with endemic, often threatened or endangered, taxa. Although these habitat correlations are recognized, it is often difficult to determine whether the taxa require extraordinary edaphic conditions, or whether they are simply tolerant of them and thrive in low competition sites. The complex interaction of physiological, genetic, and environmental factors in plant endemism has been addressed by a number of authors (see, among others: De Silva 1934; Mason 1946; Bamberg and Major 1968; Kruckeberg 1954).

Endemism may also be the product of paleoecology as well as contemporary ecology. Hooker (1862), Fernald (1925), and Hultén (1937) were some of the first botanists to analyze arctic and alpine floristic relationships and to emphasize the role of Pleistocene environments in shaping modern plant distributions. Since these early papers, a number of other authors have discussed the arctic element in the alpine flora of North America (e.g., Dahl 1946; Weber 1965; Ives 1974; Löve and Löve 1974). However, origins and dispersal routes remain most easily analyzed on the basis of individual taxa. It is not yet, and may never be, possible to describe generalized paleoecological conditions that would explain the numerous cases of disjuncts, endemics, and arctic/alpine species pairs seen in our flora.

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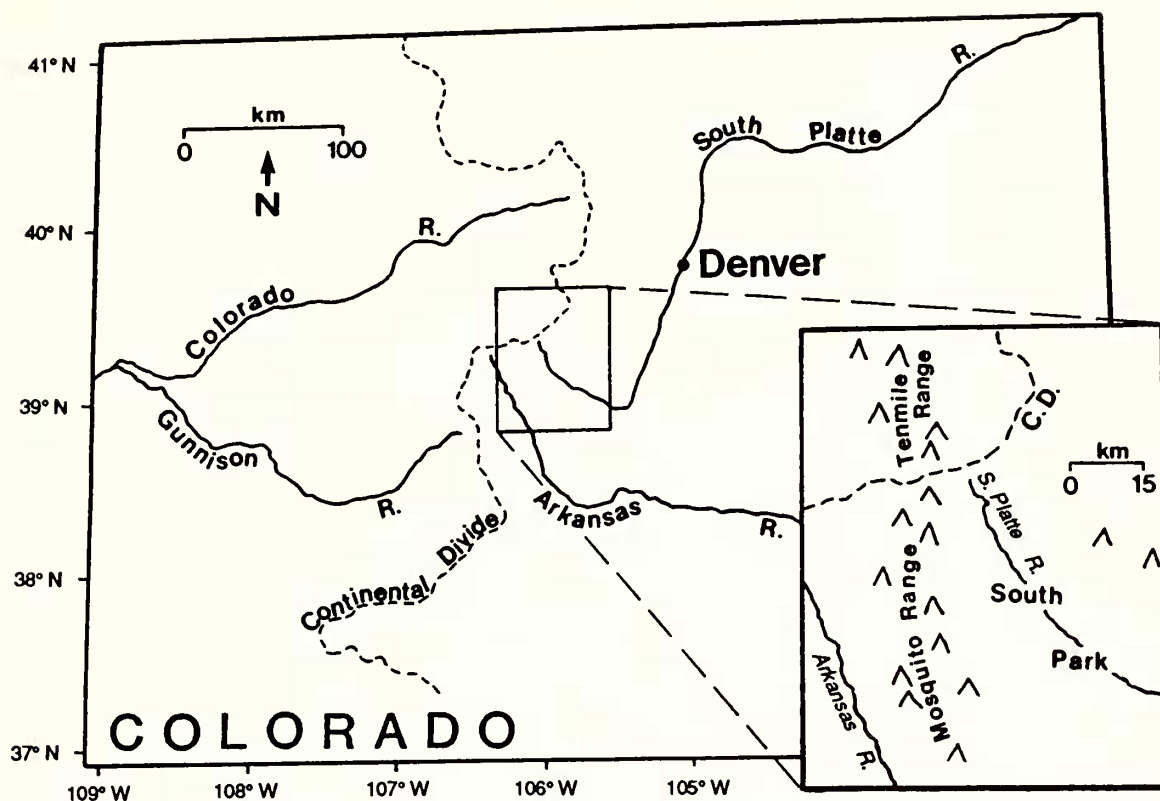


FIG. 1. Location of Mosquito Range in Colorado.

The southern Rocky Mountains contain some unusual plant distributions which provide opportunities to assess the possible contributions of edaphic and paleoecological factors in endemism. One center of phytogeographical interest is the Mosquito Range of central Colorado (Fig. 1). The range is noteworthy for its abundance of endemic and disjunct arctic and boreal plant taxa (Thorn 1981; Weber 1987, 1990). It also has an unusual abundance of carbonate bedrock rare or absent elsewhere in the Colorado mountains. The unusual flora there suggests an association with the bedrock, although this relationship has not been demonstrated definitively for any species.

Eutrema penlandii Rollins (Brassicaceae), also known as *E. edwardsii* ssp. *penlandii* (R. Br.) Weber (Rollins 1950; Weber 1990) is endemic to the Mosquito Range, with affinities to a circumpolar arctic species complex. In North America, the closest relatives are found 2000 km to the north in the Canadian Arctic Archipelago.

One phytogeographic scenario suggests that glacial advances pushed cryophilous taxa like *Eutrema* and other taxa from the Arctic to the Southern Rockies (Löve and Löve 1974). Whether this migration was in the Pleistocene, or perhaps as early as the Tertiary (Weber 1987) is arguable. Within the Mosquito Range, valley glaciers were common at different times (Capps 1909). Manley (1986) found moraines to indicate ice cover 15,000–20,000 yr BP, and extensive glacial evidence exists throughout the range. Many of the Pleistocene

moraines identified by Capps (1909) are adjacent to current populations of *E. penlandii*.

Given these conditions, it seems very unlikely that *Eutrema* could have existed in situ during the late Pleistocene. More probable habitat can be found at lower elevations in nearby South Park (Fig. 1). This high elevation (ca. 2900 m) grassland today supports other disjunct arctic and boreal species, including *Primula egaliksensis* Wormskj. and *Salix candida* Fluegge (Cooper 1991; Weber 1990). Radiocarbon dates from Lost Park bog in the nearby Tarryall Mountains indicate extensive vegetative cover there at least as early as 11,820 (± 100) yr BP (Vierling and Sullivan 1992). If *Eutrema penlandii* is a Pleistocene relict, it may have migrated up in elevation with Holocene warming and glacial retreat.

Although *Eutrema penlandii* was first discovered in 1935, detailed studies of the species were not conducted until relatively recently when the Colorado Natural Areas Program initiated habitat and population surveys. The report by Naumann (1988) suggested federal listing as a threatened species because of the few known populations, low numbers of individuals in these populations, and the restricted habitat. A primary concern was an apparent correlation with carbonate bedrock and high elevation sub-irrigated soils. Acid mine drainage in the Mosquito Range then appeared to have the potential to alter the integrity of these alpine habitats.

Appropriate management of *Eutrema penlandii* required a precise determination of the habitat, in particular, its relationship to carbonate substrate. The study described here is our assessment of the habitat characteristics of this taxon. Our objective was to look for common environmental parameters in the known populations that might at least partially explain the distribution of *E. penlandii*. We specifically addressed the following:

1. Comparison of soil pH and moisture levels within and outside *Eutrema* populations.
2. Determination of associated bedrock.
3. Comparison of levels of exchangeable calcium within and outside *Eutrema* populations.
4. Description of local geochemistry through analysis of soil oxides and trace elements.
5. Determination of associated bryophyte taxa.

The close association of *Eutrema* and bryophytes was noted by Naumann (1988) as a consistent feature of the known populations; however, these bryophyte species were never collected or identified. Because at least some bryophytes are known to be good indicators of soil pH, we believed it critical to have identifications of all associated taxa.

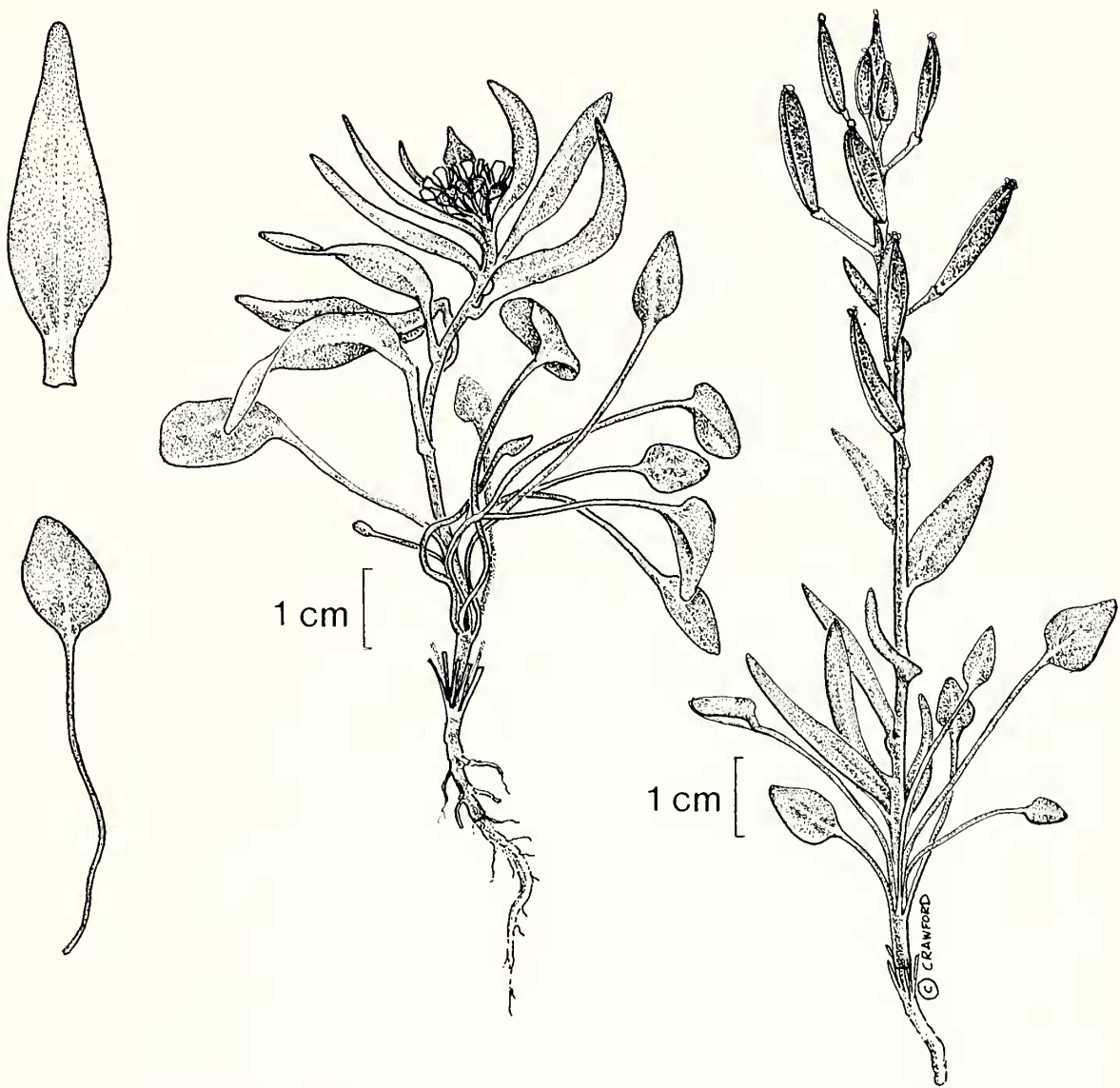


FIG. 2. *Eutrema penlandii*.

STUDY SITES AND METHODS

Species description. *Eutrema penlandii* is an inconspicuous herbaceous perennial 2–10 cm high (Rollins 1950). It is distinguished from other white-flowered alpine members of the Brassicaceae by its glabrous nature, ovate, thinly petiolate basal leaves, sessile cauline leaves, and its elliptical quadrangular fruits (Fig. 2). Plants grow singly or in clumps of 2–5 individuals in a bryophyte or bryophyte-graminoid community. There is no evidence of vegetative reproduction. Populations contain from 50–2000 individuals and cover from 0.5 to ca. 16 ha in area (Naumann 1988).

Study sites. We used the eight previously documented populations of *Eutrema penlandii* (Naumann 1988) in the Mosquito Range between Hoosier Ridge and Mount Sherman for analysis. Within this area, *E. penlandii* is restricted to low angle east and south-facing

slopes between 3745 and 3939 meters. Deep snow accumulation on these leeward slopes provides persistent snowbeds lasting into July. Snowbed meltwater supports the bryophyte understory that is one of the few common elements among *Eutrema* populations.

Geological maps of the region (Tweto 1974; Tweto et al. 1978) indicate that *Eutrema penlandii* can be found on a number of geological formations, only some of which contain carbonates. These include the Minturn Formation (sandstone, shale, and scattered carbonates), the Belden Formation (shale, carbonates, and sandstone), Leadville Dolomite, the Maroon Formation (sandstone, mudstone, and conglomerate), and intrusive porphyries. The bedrock of the region is highly diverse; because most *Eutrema* populations occur below scree slopes, different formations can contribute to the underlying substrate.

Populations were studied in the field between 6 July 1991 and 30 July 1991 when flowers were in bloom; laboratory analyses were completed between July 1991 and January 1992.

In the field we measured slope and aspect, and flagged individual plants for population counts and determination of boundaries. Indicator mosses were collected in each population and sent to the University of Colorado Museum Herbarium (COLO) for identification. We collected 3 to 5 soil samples adjacent to *Eutrema* plants at a depth of 10 cm; samples were spaced equidistantly throughout the population. An equal number of control samples were taken 2–20 m outside each population. For sampling purposes, we treated subpopulations as distinct communities because they occurred several hundred meters apart. Location for peripheral samples was determined on the basis of the nearest floristically distinct plant community (defined as a change from bryophyte and bryophyte-graminoid community to a forb-dominated community). Due to the frequent occurrence near *Eutrema* populations of boulderfields, cliffs, standing water, and other sites inappropriate for comparative soil samples, we could not use a uniform sampling distance. Given the mosaic nature of these alpine habitats, we believe that subjective sampling using phytosociological criteria would provide the most useful comparison of botanically significant soil characteristics.

Analysis. In the laboratory, wet soil weight was measured immediately, and dry soil weight was measured after air drying for 48 hours when no further weight change was indicated. Soil moisture was calculated as: weight soil water/dry soil weight. After sieving out organic materials to ensure homogeneity, we mixed a 1:1 ratio of soil and distilled water, let the mixture settle for 20 minutes, then measured soil pH with an electronic pH meter. Exchangeable calcium was analyzed in a Varian 227B AA/AE Atomic Absorption Spectrometer following preparation procedures adapted from Moore and Chapman (1986).

To measure oxides and trace elements in the soil, samples were weighed, dried at 1100° overnight, and reweighed. They were then sieved to separate stones and undecomposed organic material, then ground to a powder. One g of powder was mixed with 9 g lithium tetraborate, fired at 1100° for 20 minutes to form a glass pellet, then analyzed using a Rigaku 3070 Spectrometer.

For statistical analysis, a log transformation of pH data was performed to compare mean pH with a two-tailed t-test (Sokol and Rohlf 1969). We also used two-tailed t-tests to measure the degree of difference between means of soil moisture and exchangeable calcium inside populations to the means in peripheral areas.

RESULTS

Twenty-two different bryophyte taxa representing 19 genera were identified in *Eutrema* populations. These were generally common alpine/subalpine taxa with no known affinity for unusual substrates, including *Mnium blyttii* B.S.G., *Didymodon asperifolius* (Mitt.) Crum, Steere and Anderson, *Aulacomnium palustre* (Hedw.) Schwaegr., *Entodon concinnus* (DeNot.) Paris, and *Bryum* spp. One species, *Brachythecium turgidum* is a calciphile (Vitt 1988), but was found only in populations at two locations.

The results of soil pH analyses are summarized in Table 1. Although t-tests on transformed data (Sokol and Rohlf 1969) show a slight statistical difference between samples within and around *Eutrema* populations ($P < 0.04$), the pH ranges are quite broad. Within populations, the pH of 48 samples ranged from 5.5 to 7.0, generally slightly acidic to neutral. Only 6 samples had a pH greater than 7, with a high of 7.9. Peripheral samples had a slightly broader range (4.6 to 8.0), from acid to alkaline.

Soil moisture levels are summarized in Table 1. Soils within populations ranged from 47% to 668% (with an outlier at 1660%), and peripheral samples ranged from 11% to 217%. Mean soil water content within populations was 338%, significantly higher than the mean of 75% found in peripheral samples (t-test, $P < 0.001$). However, the high variance of these soil moisture levels limit their usefulness for interpretation; the only significant result that we can conclude is that *Eutrema* is only found in sites that are consistently very wet; high moisture levels may be maintained at least in part by the associated bryophytes.

Exchangeable calcium varies a great deal within and around populations (Table 1). Samples within populations have a range of 1550–15,500 ppm, with a mean of 5800 ppm. Calcium in peripheral samples ranged from 155–10,850 ppm, with a mean of 3400. Although these means are statistically different (t-test, $P < 0.001$) the high variance and comparison with the potentially much greater levels of calcium in other known carbonate soils (Bowen 1966; Bam-

TABLE 1. HABITAT CHARACTERISTICS OF *EUTREMA PENLANDII*. P value represents 95% CI for t-test using log transformation of data.

	Within populations	Peripheral samples	P value
Soil pH			
Mean (SE)	6.33 (0.08)	6.05 (0.11)	<0.04*
Range	5.50–7.90	4.60–8.00	
n	48	41	
% Soil Moisture			
Mean (SE)	338.4 (52.1)	74.7 (11.0)	<0.000**
Range	47.0–1660.0	11.0–217.0	
n	31	29	
Exchangeable Calcium (ppm)			
Mean (SE)	5649 (443)	3365 (393)	<0.001**
Range	1178–15,500	155–10,850	
n	44	39	
Soil Composition			
(n = 5; Samples taken from Pennsylvania Mt., Mosquito Pass, Mt. Sherman, Mt. Silverheels, and Hoosier Ridge <i>E. penlandii</i> populations)			
Oxide	Mean % (SE)	Element	Mean ppm (SE)
NO ₂	0.77 (0.34)	V	49.6 (10.7)
MgO	1.14 (0.15)	Cr	68.6 (27.7)
Al ₂ O ₃	11.34 (0.73)	Co	8.8 (3.2)
SiO ₂	45.20 (3.44)	Zn	133.6 (16.3)
P ₂ O ₅	0.33 (0.05)	Rb	114.6 (8.9)
K ₂ O	2.55 (0.15)	Sr	181.0 (41.6)
CaO	1.92 (0.21)	Y	7.0 (2.3)
TiO ₂	0.39 (0.06)	Zr	151.4 (13.5)
MnO	0.10 (0.02)	Nb	13.4 (1.3)
FeO ₃	3.04 (0.57)	Ba	825.4 (226.0)

berg and Major 1968; Retzer 1974) suggest that *Eutrema* populations are not limited by the presence or absence of high levels of calcium.

The oxide and trace element composition of soils also appears to vary a great deal (Table 1). All levels are comparable to typical alpine soil profiles (Bowen 1966; N. Bower personal communication) and there is no indication of unusual geochemistry that would explain the endemism of *E. penlandii*.

DISCUSSION

Based on analyses of soil composition, pH, and available calcium, we cannot conclude there is any direct correlation between the occurrence of *Eutrema penlandii* and the presence of carbonate bedrock in the Mosquito Range. While we did find differences in soil pH and calcium levels between samples within and around *Eutrema*

populations, the range of values suggests that these parameters may not be biologically significant. Acidic to neutral pH values are typical for Colorado alpine soils (Johnson and Cline 1965). On carbonate parental material, pH sometimes reaches slightly alkaline levels but these may be buffered by organic acids in the peat in which *Eutrema* grows. The highly variable amounts of exchangeable calcium are low in comparison to other known carbonate soils (Bowen 1966).

Trace elements and oxide analyses give no indication of the presence of chemically anomalous substrate, and we can find no consistent correlation of the presence of *Eutrema* with any specific geological formation. While sometimes found on or near carbonate-rich bedrock (Manitou Dolomite, Belden and Minturn Formations), it is found equally often on other formations that do not contain carbonates.

Although this species is apparently *not* an obligate calciphile, there are other critical aspects of the habitat that may restrict its distribution. The consistently high moisture levels in *Eutrema* habitat suggest that continually wet soil may be one of the most important.

Low angle, high elevation leeward slopes are not common in the central Rockies; for example, both the adjacent Ten Mile and Collegiate Ranges have elevations comparable to those in the Mosquito Range, but the former generally contain steep, unstable lee slopes where snow does not accumulate deeply. In addition, these ranges are oriented more north-south than the Mosquito Range, which has a northeast-southwest trend. As Weber (1987) noted, this orientation results in slower snow melt and more available moisture in the growing season, as well as winter protection from desiccating chinook winds.

Accumulation of deep snowfields is a critical aspect of *Eutrema* habitat: these snowfields provide a constant source of moisture that nourishes bryophyte communities. The mat of bryophytes in turn holds moisture and provides a cold, continually wet microsite necessary for *Eutrema* populations. *Eutrema* also appears to prefer sites with low competition from other forbs. This combination of factors is uncommon even in the Mosquito Range. As a result, the rarity of *Eutrema* populations may be due to the limited amount of appropriate microhabitat even though there are broad expanses of south and east-facing slopes.

CONCLUSIONS

Whatever its origin, *Eutrema penlandii* is a striking reminder of the complex affinities of the Colorado flora. We find no evidence from this comparative study of the few known populations of *Eutrema penlandii* that it is restricted in its distribution by dependence on alkaline bedrock or unusual geochemistry. This should encourage

botanists to continue to look for it elsewhere in the central Rockies. However, based on what we have observed, the species does appear to be dependent on the availability of wet, low angle, low competition, high elevation sites. An intensive search for additional populations of *E. penlandii* in the summer of 1991 by numerous personnel from the Alma American Mining Company and the Colorado Native Plant Society neither revealed significant new populations in the Mosquito Range or surrounding mountains, nor led us to reassess the low population numbers given in the original status report.

We find the few populations, low numbers of individuals, and apparent sensitivity to moisture availability in this species reason for concern, especially as our global climatic uncertainties may add further stress to plant taxa already restricted to sensitive microhabitats. As Schoonmaker and Foster (1991) suggest, paleoecological histories can have considerable relevance for understanding contemporary ecological changes. While *Eutrema penlandii* is only one of the many species in the Mosquito Range with individual histories and individual ecologies, we suggest that it is an important one that deserves habitat protection. This species, and the Mosquito Range flora as a whole, warrant future attention from ecologists and phytogeographers.

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